

Growth and yield of barley in relation to grasshopper feeding damage

Sultan H. Begna¹ and Dennis J. Fielding^{2,3}

¹Vancouver, British Columbia, Canada; and ²Subarctic Agricultural Research Unit, USDA/ARS, P.O. Box 757200, University of Alaska, Fairbanks, Alaska 99775, USA. Received 5 April 2006, accepted 17 September 2007.

Begna, S. H. and Fielding, D. J. 2008. Growth and yield of barley in relation to grasshopper feeding damage. Can. J. Plant Sci. **88**: 219–227. Grasshoppers are common pests of barley (*Hordeum vulgare* L.) in subarctic Alaska and cause substantial crop loss during outbreaks, but there is little information about the growth response of barley to grasshopper feeding damage. In two growth chamber experiments, we studied the effect of four densities (0, 1, 2, and 3 pot⁻¹, equivalent to 0, 25, 50 and 75 grasshoppers m⁻²) of grasshoppers (*Melanoplus sanguinipes* F.) on the above- and below-ground growth of barley (eight plants per pot). Plants were exposed to grasshoppers beginning in the 3rd to 4th leaf stage (exp. 1) and in 1st to 2nd leaf stage (exp. 2). Plants were harvested and growth variables were measured shortly after anthesis and at maturity. Generally, the reduction in above-ground dry matter, at the highest density was 29 and 47% for exp. 1 and exp. 2, respectively. Effects of grasshoppers on below-ground growth (dry matter and surface area of roots) was less consistent than on above-ground variables; however, at the highest grasshopper density in exp. 2, dry matter and surface area of roots were reduced by about 40–53%. Grain yield (pooled over experiments) decreased by 19 and 36% for grasshopper densities of 2 and 3 pot⁻¹, respectively. Most of the yield loss was accounted for by reduced seed weights, while protein content per seed remained nearly constant. The proportion of total above-ground dry matter represented in harvested grain and root:shoot ratios were not affected by grasshopper feeding. These results provide greater understanding of plant responses to insect feeding damage and will lead to more accurate estimates of economic injury levels.

Key words: Crop yield loss, economic injury level, harvest index, Insecta

Begna, S. H. et Fielding, D. J. 2008. Croissance et rendement de l'orge selon les dommages causés par la sauterelle. Can. J. Plant Sci. **88**: 219–227. Les sauterelles parasitent couramment les champs d'orge (*Hordeum vulgare* L.) dans les zones subarctiques de l'Alaska. Durant les infestations, elles causent des pertes substantielles aux cultures, mais on sait peu de choses sur la réaction de l'orge à de tels dommages au niveau de la croissance. Les auteurs ont étudié l'incidence de quatre densités (0, 1, 2 et 3 insectes par pot, soit l'équivalent de 0, 25, 50 et 75 par m²) de sauterelles (*Melanoplus sanguinipes* F.) sur la croissance des organes aériens et souterrains de l'orge (huit plants par pot), lors de deux expériences en chambre de croissance. Ils ont récolté les plants et mesuré les variables de la croissance peu après l'anthèse ainsi qu'à maturité. Dans l'ensemble, la réduction de la concentration de matière sèche dans les organes aériens s'est respectivement établie à 29 % et à 47 % lors de la première et de la deuxième expérience, à la densité la plus élevée des ravageurs. Les sauterelles ont une incidence moins cohérente sur la croissance des organes souterrains (concentration de matière sèche et superficie des racines) que sur la croissance des organes aériens. Néanmoins, lors de la deuxième expérience, à la densité de sauterelles la plus élevée, les auteurs ont noté une baisse de 40 % à 53 % de la concentration de matière sèche et de la superficie des racines. Le rendement grainier (global pour les deux expériences) diminue de 19 % et de 36 % à la densité de 2 et de 3 sauterelles par pot. La majeure partie de cette baisse est attribuable au poids réduit des graines, la concentration de protéines dans la graine demeurant pratiquement la même. La proportion de matière sèche dans les organes aériens que représentent le grain récolté et le ratio racines:pousses n'est pas affectée par les dommages que cause la sauterelle. Ces constatations nous aident à mieux comprendre la réaction des plantes à l'alimentation des insectes et permettront d'estimer plus précisément les pertes économiques qui en résultent.

Mots clés: Perte de rendement agricole, importance des pertes économiques, indice de récolte, insectes

Grasshoppers are one of the most important insect pests of agricultural crops throughout the world (Wright 1986; Gangwere et al. 1997). In North America, grasshoppers have caused an estimated average annual crop loss of \$6 million to cereal crops, with losses as high as \$200 million in an outbreak year in Canada and the United States of America (Gage and Mukerji 1978). One

of the most serious grasshopper pest species in North America is the migratory grasshopper, *Melanoplus sanguinipes* Fabricius. (Pfadt 1994). The migratory grasshopper is distributed north to central Alaska and south to the tropical lowlands of Mexico (Hebard 1929; Alexander 1941; Vickery and Kevan 1983). In the United States of America, the migratory grasshopper causes more crop damage than any other species of grasshopper (Pfadt 1994).

Damage occurs most frequently on grasslands, although crops, particularly young seedlings of cereals,

³ To whom correspondence should be addressed (e-mail: ffdjfl@uaf.edu).

are very susceptible (Begna and Fielding 2003). The degree of damage inflicted on crops by grasshoppers depends on many factors, such as number of grasshoppers, their size and feeding rate, weather conditions, and plant vigor. Yield losses result from the reduction of photosynthetic tissue as the grasshoppers feed on leaves, and from head clipping when grasshoppers chew through the peduncle. Depending on the time of defoliation, reduction in photosynthetic capacity can reduce the overall growth of the plant, reduce the number of fertile spikelets at pollination, and reduce the amount of photosynthate available for grain filling (Ryle and Powell 1975; Olfert and Mukerji 1983; Aggarwal et al. 1990; Jenkyn and Anilkumar 1990).

Root growth and morphology can also be affected by defoliation, but far less is known about the below-ground plant system than above-ground, particularly in relation to insect damage. Any damage that occurs on the above-ground plant parts may ultimately change the root system and subsequent nutrient-water uptake, thus slowing recovery from the damage, diminishing the crop's ability to compete with weeds, and reducing final yield.

Several studies in temperate and tropical regions have been conducted to determine the relationship between grasshopper density, damage, plant growth, and yield loss in crops and rangelands (Pickford and Mukerji 1974; Capinera and Roltsch 1980; Olfert and Mukerji 1983; Wright 1986; Olfert and Slinkard 1999). In studies of defoliation of small grains, the most common treatment is a one-time defoliation (Ryle and Powell 1975; Mukerji et al. 1976; Olfert and Mukerji 1983; Sharrow 1990; Begna and Fielding 2003). One-time defoliation may mimic the effects of a sudden influx of adult grasshoppers, which are then chemically controlled. However, a more typical situation in Alaska may be chronic defoliation occurring over time, such as when crops are seeded in infested stubble or there is a steady migration into the crop. Furthermore, most of these studies have only measured reduction in final yield without consideration of the manner in which the whole plant responds to feeding damage. Without an understanding of how the whole plant reacts to feeding damage, it is difficult to develop robust models of insect damage/yield loss relationships. Previous field studies in Alaska have quantified many aspects of the allocation of photosynthates to above-ground plant organs in relation to grasshopper feeding (Begna and Fielding 2005). The objective of this study was to examine in more detail in controlled environment chambers, the responses of barley (*Hordeum vulgare* L.) plants to chronic defoliation by grasshoppers, including root growth and allocation of nitrogen to grain and other above-ground parts.

MATERIALS AND METHODS

Barley plant responses to feeding by grasshoppers were studied within a controlled environment chamber at the University of Alaska Fairbanks. Seeds (barley cultivar

Otal) were planted directly into sand held in plastic growing pots (irregular octagons with 0.037 m² cross-sectional area and 0.4 m depth). Sand was chosen because it facilitates the extraction and cleaning of roots for measurements. To provide plants with adequate nutrients, we used 3.5 g 15-9-12 NPK controlled-release fertilizer per pot, which also contained all essential macro and micronutrients (Osmocote, Hummert, Int., Earth City, MO). Seedlings were thinned to eight plants per pot resulting in a plant density equivalent to field conditions (216 plants m²). Grasshopper densities of 0, 1, 2, and 3 pot⁻¹ (~0, 27, 54 and 81 grasshoppers m⁻², spanning extreme values found in the field) were used. Cages were stocked with 3rd to 4th instars of a non-diapausing strain of *M. sanguinipes* when plants were at the 2nd to 3rd leaf stages (Haun 1973), 25 d after planting (DAP) in exp. 1 and, in the second experiment, at the 1st to 2nd leaf stages, 10 DAP. This approximates the coincident phenologies of crop and grasshoppers in central Alaska. Grasshoppers in cages were checked at least three times week and dead grasshoppers replaced to maintain the desired number of grasshoppers per pot. A randomized complete block design with three blocks was used in each experiment.

Temperature and photoperiod conditions of the chamber approximated interior Alaska field conditions in the summer. Cool-white, very high output (VHO) fluorescent lamps and 100 W incandescent lamps provided 250–350 µmol m⁻² s⁻¹ photosynthetic photon flux (PPF) at the top of the canopy inside the cages, as measured with a PAR-meter (Basic Quantum Meter, Spectrum Technologies, Inc, Plainfield, IL). New lamps were installed at the beginning of the first experiment. Photoperiod was approximately 20 h, which provided enough light for plant growth. During clear days in interior Alaska (latitude 64°N) near the summer solstice, sunlight provides a mean PPF of about 500 µmol m⁻² s⁻¹ (Bonanza Creek Long-Term Ecological Research 2001). Even though the instantaneous PPF levels were lower than the mid-day PPF peak levels in the field, the daily-integrated PPF levels are typical of field values in interior Alaska. Partly cloudy days are very typical of the early summer weather patterns in interior Alaska. Furthermore, Chabot et al. (1979) showed that leaf anatomy and photosynthesis are more influenced by the daily-integrated PPF than peak PPF. Relative humidity was around 50%. Diurnally fluctuating temperatures approximated mean daily highs and lows of the growing season of interior Alaska: minimum temperature of 10°C for 8 h, with temperatures increasing linearly to a maximum of 24°C, which was held for 2 h before decreasing linearly to the minimum temperature. Internal body temperatures of the grasshoppers were likely to be higher than ambient temperatures during the photophase because they were able to thermoregulate by climbing to the top of the cages (about 30 cm from the lights) and absorb thermal radiation from the incandescent lamps.

Two harvests were conducted in each experiment; at 55 and 78 DAP in exp. 1, and 64 and 78 DAP in exp. 2. For unknown reasons, the plants in the second experiment developed somewhat more slowly than those in the first. In both experiments, the first harvest occurred 5–8 days after 50% anthesis, and the final harvest at maturity. Plants were separated into leaves, stems, roots and grain. Leaves were separated at the collar from the stem. Senescence/dead and dropped leaves were collected as much as possible and included to the final leaf dry weight to determine production of above-ground biomass. Leaf area (cm^2), using only intact leaves, was measured at the first harvest with a Li-Cor 3000 Model Leaf Area Meter. Plant materials were dried for 24 h at 60°C and the dry weight of each fraction was determined. Then plant parts, excluding roots, were ground and about 200 mg of each sample was analyzed with a LECO 2000 CHNS analyzer for dry combustion determination of total C and N concentration in plant tissues. Harvest indices based on dry matter and nitrogen content within the plant were calculated as the proportion of total above-ground dry matter (or nitrogen) in the grain at maturity.

Roots were gently separated from the growing media by immersing the whole pot in water and gently loosening the sand and roots together out of the pots. Once the whole root mass was out of the pot about 80% of the root system could be collected simply by floating them in a large quantity of water. A 0.3-mm-diameter sieve was used to separate the remaining roots from the sand and water. The whole root system of each pot was cut into about 15-mm segments and put in glass jars filled with water. Jars were then shaken (Model 6000 Eberbach Shaker, Eberbach, Corp.) for about 15–20 min to mix root segments. After removing the water from the jars excess water from the roots was removed using paper towels.

Root surface area was estimated using scanner-based image analysis software (WinRHIZO version 5.0, Regent Instruments, Quebec, QC). Two subsamples (10% each by fresh weight) of the total root were used for analysis. Roots were scanned on an optical scanner [Epson Expression Scanner, 1600 dots per in (667 dots per cm) resolution]. The scanner was equipped with an overhead light source to eliminate shadows. Root subsamples were left in a petri dish filled with toluidine blue stain (0.1% wt/vol) for about 10 min (Costa et al. 2000) to enhance scanner imaging. After immersion, excess stain was removed from the roots by rinsing them under running tap water for about 1 minute (Costa et al. 2000). Root samples were placed in the Plexiglas trays (20 by 30 cm) with a 0.3 to 0.4 cm deep layer of distilled water, and the water was used to untangle the roots as much as possible in order to minimize root overlapping and crossing over (Costa et al. 2000). The average of those two subsamples was used for treatments comparisons. The remaining root material was oven-dried for 24 h at 60°C for dry weight determination. Dry weights

were adjusted to compensate for the 20% of the root mass used for the surface area measurements.

All measurements were expressed on a per-pot basis. The relationship between grasshopper density and dry matter measurements, yield components, and percentage nitrogen of barley was evaluated using analysis of covariance (ANCOVA), with grasshopper number as a continuous covariable and experiment as a class variable (PROC GLM, SAS Institute, Inc. 2002). No transformations were applied to any of the variables, including percentage N and ratio variables, because none were found to be severely non-normal (Shapiro-Wilkes $W > 0.85$, PROC UNIVARIATE, SAS 2002), and transformations did not alter results.

Translocation of dry matter and nitrogen from non-grain parts to the developing grain was assessed by weight loss in the non-grain tissues between anthesis and maturity. Respiration, consumption by grasshoppers, and dropped leaves may have accounted for some of the loss, but we assumed that weight loss was proportional to the amounts translocated to the developing grains (Gallagher et al. 1976).

The relationship between numerator and denominator of all ratio variables, e.g., harvest indices, percentage weight loss between anthesis and maturity, and root:shoot ratios, was checked for isometry (intercept not significantly different from zero and a linear slope). Furthermore, results of analyses using the ratio variables were compared with results obtained with ANCOVA, with the denominator as a covariable and the numerator as dependent variable. All ratio variables were found to be isometric and results did not differ qualitatively from direct analyses of the ratios (although significance levels differed somewhat, with the ANCOVA generally resulting in greater F-values for the independent variables). Therefore, results of the analyses using ratio variables are presented here.

RESULTS

Grasshopper Damage on Above-ground Plant Parts

Grasshopper damage significantly altered most measures of plant growth and development (Table 1). Grasshopper feeding reduced leaf area by an approximately equal amount in both experiments (Fig. 1). Visual observations revealed that leaves and awns were most heavily damaged, and stems were fed upon only slightly. Medium and high grasshopper densities reduced leaf area by 36 and 54%, respectively, at anthesis in exp. 1, and by 25 and 38%, respectively, at anthesis in exp. 2 (Fig. 1). Above-ground dry matter declined with increasing grasshopper density (Fig. 2a, b). At first harvest, shortly after anthesis, the highest grasshopper densities reduced total aboveground dry matter by 38 and 34% in exps. 1 and 2, respectively.

There was a significant interaction effect between grasshoppers and experiment on the percentage loss of

Table 1. Analysis of covariance on growth parameters of potted barley plants (eight plants per pot) subjected to grasshopper feeding damage (0, 1, 2, or 3 grasshoppers per pot). Measurements were taken at anthesis and at maturity. There were three replicates per experiment, and experiment was repeated once. (d.f. = 1, 20 in each case)

Dependent variables	Experiment	Covariable Grasshoppers	Interaction E × G
Leaf area (anthesis)	0.7	17.2**	0.2
Dry weight above-ground (anthesis)	3.3	21.0**	0.4
Dry weight above-ground (maturity)	13.7**	46.6***	1.9
% weight loss (anthesis to maturity)	0.1	0.5	7.8*
Dry weight grain	1.1	33.8***	1.1
Number of seeds per pot	15.4**	14.4**	0.0
Harvest index (dry matter)	76.3***	0.1	11.3**
Dry weight roots (anthesis)	24.2***	17.8**	1.8
Dry weight roots (maturity)	16.2**	16.0**	1.4
Root Surface Area (anthesis)	10.9**	2.2	0.9
Root Surface Area (maturity)	8.3*	19.3**	1.7
Root:Shoot ratio (anthesis)	16.9**	3.3	0.1
% Weight loss, roots (anthesis to maturity)	1.7	0.0	14.3**
% N Above-ground dry matter (anthesis)	5.2*	14.8**	0.1
% N Above-ground dry matter (maturity)	56.7***	24.5***	0.2
% N Grain (maturity)	2.7	18.1**	0.8
Total N in grain	0.0	11.6**	0.3
N per kernel	27.2***	0.8	0.0
% Loss of N (anthesis to maturity)	4.4*	0.4	2.6
Harvest index (N)	324.8***	14.1**	2.2

*, **, *** $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively.

above-ground dry matter between anthesis and maturity (Table 1). In the first experiment, grasshoppers did not have a significant effect on the percentage difference in dry matter between anthesis and maturity, whereas in the second experiment, plants lost increasing percentages of dry matter with greater numbers of grasshoppers (Fig. 2c).

Grain yield declined with increasing grasshopper densities (Fig. 3a), but did not differ significantly between experiments (Table 1). The number of seeds declined with increasing grasshoppers in both experiments (Fig. 3b). Grain yield was reduced in exp. 1 by 21 and 28% at medium and high grasshopper density

levels, respectively, and by 16 and 43% in the second experiment (Fig. 3a). The harvest index was greater in the second experiment than in the first, averaging 46 and 56% in exps. 1 and 2, respectively, over all grasshopper densities. There was a significant interaction effect between experiment and grasshoppers on the harvest index (Table 1). In the first experiment, regression of harvest index on grasshoppers was not significant ($P > 0.10$). In the second experiment, the increase in harvest index with increasing grasshopper numbers was statistically significant, although the nearly horizontal slope indicated that the effect was of little practical significance ($HI = 0.55 + 0.0084x$, $r^2 = 0.41$, $P = 0.026$).

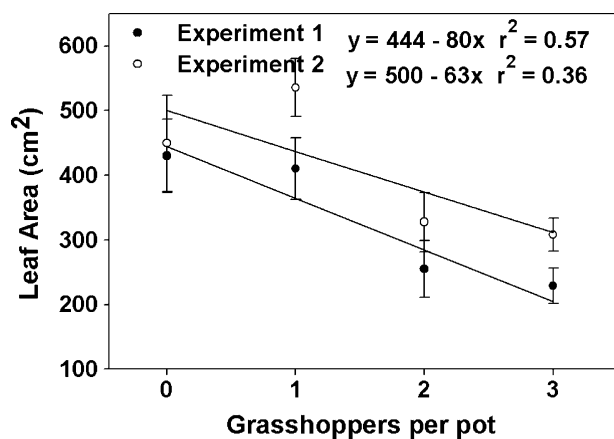


Fig. 1. Regression of leaf area of barley at anthesis on number of grasshoppers per pot. Each point is the mean of three observations, vertical bars represent SE.

Grasshopper Damage on Below-ground Plant Growth

Grasshopper feeding also affected root growth (Table 1). Root mass at anthesis declined with increasing numbers of grasshoppers in both experiments (Fig. 4a), but at maturity, the regression of root mass on grasshopper numbers was not significant in the first experiment (Fig. 4b). At the highest grasshopper levels at anthesis, below-ground dry matter was reduced by 34% in exp. 1, and by 29% in exp. 2.

Even though roots were not directly consumed by grasshoppers as were the above-ground parts, the root:shoot ratio was not significantly affected by grasshopper feeding at anthesis (Table 1). Root:shoot ratios were greater in exp. 1 than in exp. 2. At anthesis, mean root:shoot ratio, averaged over all grasshopper treatments, was 0.71 in exp. 1, and 0.55 in exp. 2. At maturity, mean root:shoot ratios were 0.52 and 0.36, for

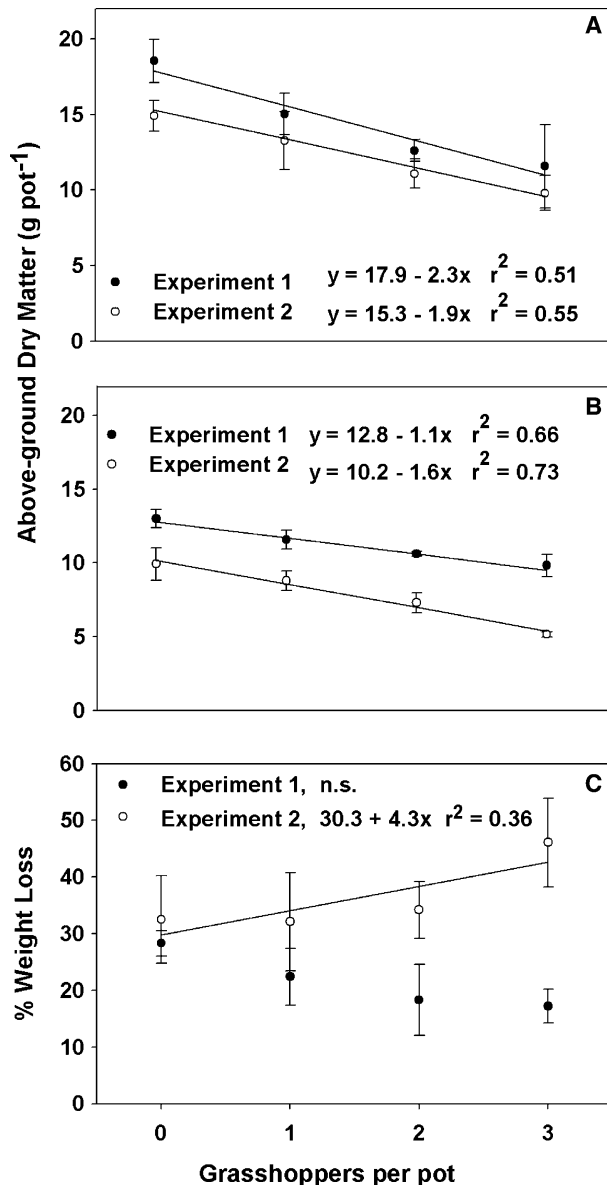


Fig. 2. Regression of above-ground dry matter of barley plants, excluding grain on number of grasshoppers per pot. A) at anthesis; B) at maturity; C) difference in above-ground dry matter between anthesis and maturity as a percentage of dry matter present at anthesis. Each point is the mean of three observations, vertical bars represent SE.

exps. 1 and 2, respectively. Patterns in the loss of root biomass between anthesis and maturity were similar to those for above-ground dry matter. Grasshoppers had no significant effect on the percentage loss of root biomass in the first experiment, but in the second experiment, percentage loss of root biomass increased with increasing grasshoppers (Fig. 4c).

Root surface area did not show a consistent pattern in relation to grasshopper defoliation. At anthesis, grasshoppers did not have a significant effect on surface area

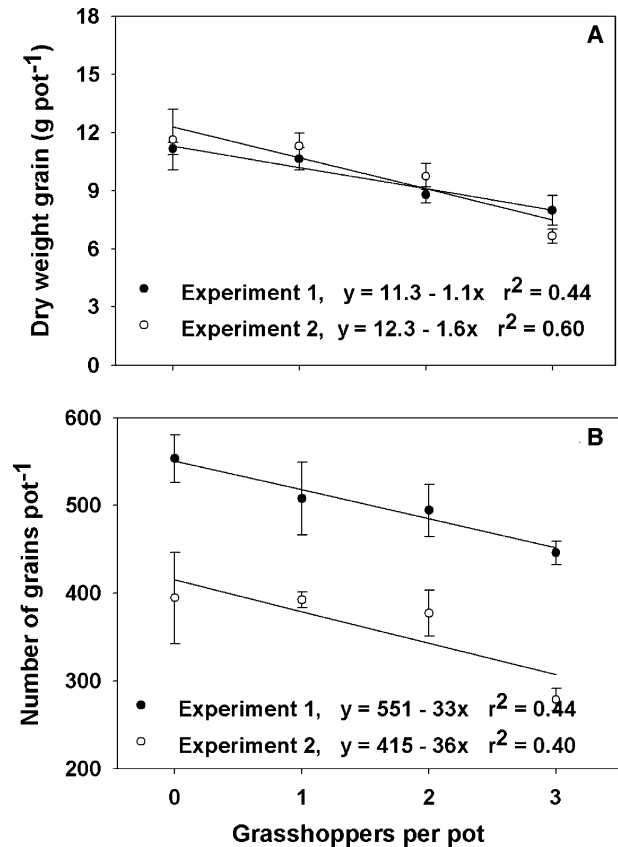


Fig. 3. Regression of dry weight grain yield (A), and number of grains per pot (B) on number of grasshoppers per pot. Each point is the mean of three observations, vertical bars represent SE.

(Table 1). At maturity, grasshoppers were associated with reduced root surface area in the second experiment only (Fig. 4D). The reduction in root surface area at the highest grasshopper density level of the final harvest of exp. 2 was 49%.

Nitrogen Balance of Above-ground Plant Parts

Generally, percentage N increased with increasing grasshopper damage for above-ground dry matter and grain (Fig. 5). Percentage N in the grain increased with grasshopper density in both experiments, a result of decreasing dry matter in the grain as opposed to increasing N content. The absolute amount of nitrogen in the grain declined with increasing grasshopper density ($\text{mg N} = 178 - 15.3 \text{ grasshoppers}$, $r^2 = 0.36$, $P = 0.002$, $N = 24$). Nitrogen per kernel (by weight) remained relatively constant with increasing grasshopper damage, but differed between experiments (Table 1). Nitrogen per kernel was higher in the second experiment (0.32 and $0.43 \text{ mg kernel}^{-1}$, for exps. 1 and 2, respectively, averaged over all levels of grasshoppers).

Above-ground N content (excluding grain) declined between anthesis and maturity to a greater degree, on a

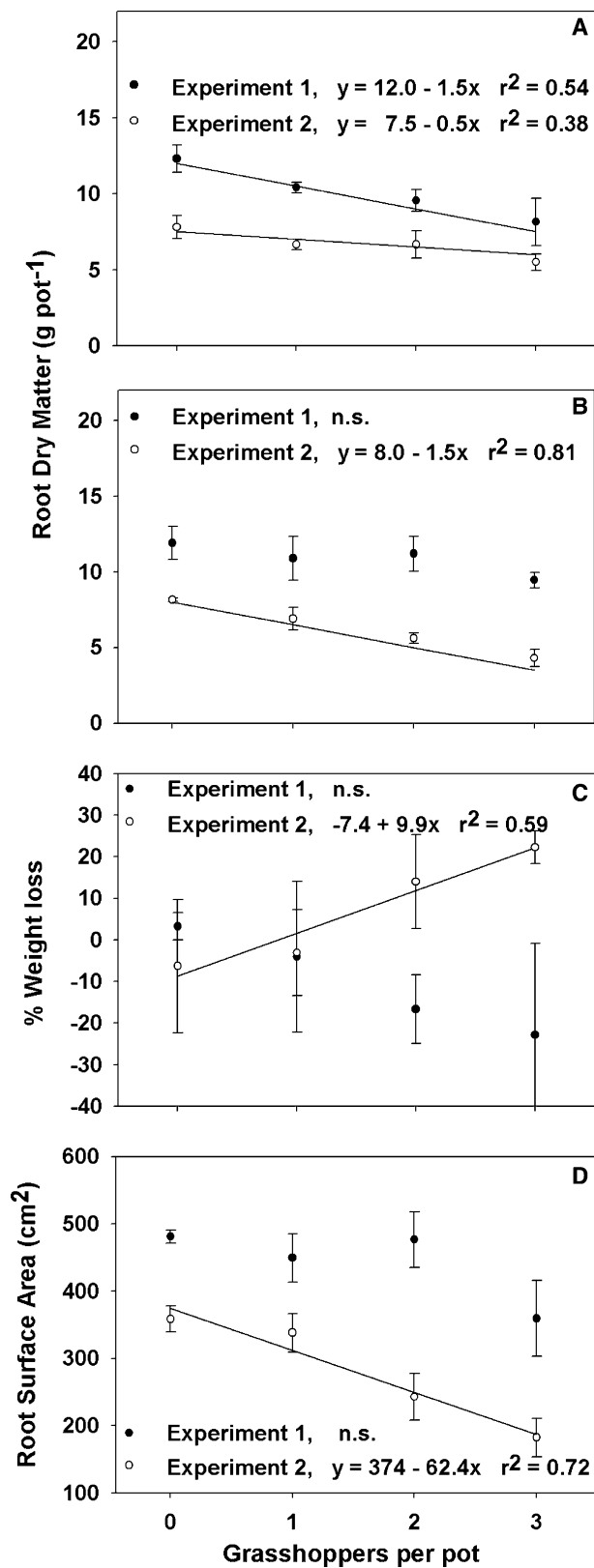


Fig. 4 (Continued)

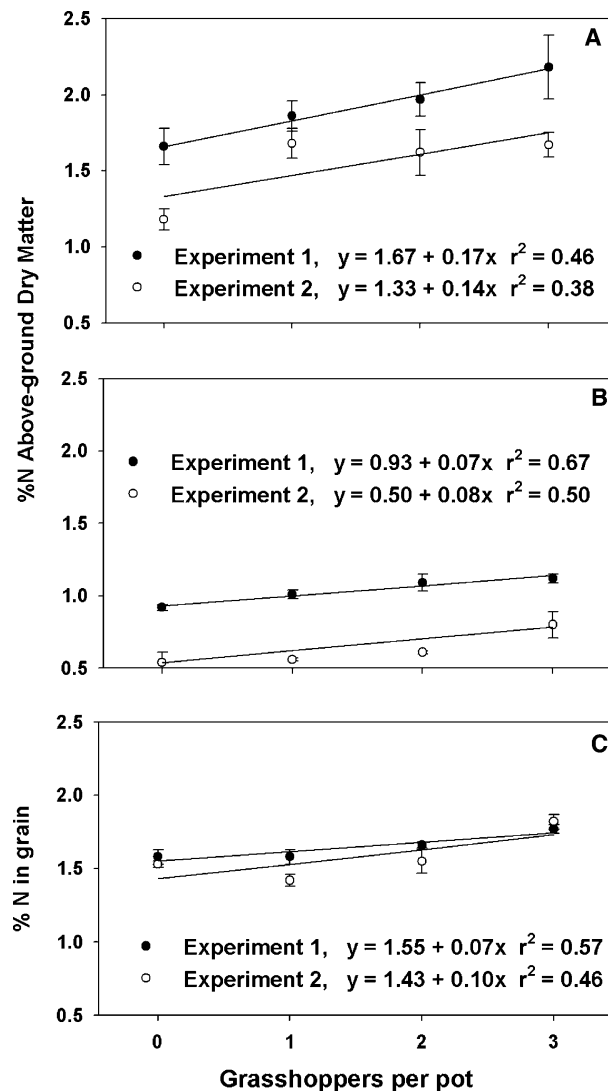


Fig. 5. Regression of percentage nitrogen of non-grain above-ground portions of barley plants (A, at anthesis; B, at maturity) and of grain at maturity (C) on number of grasshoppers per pot. Each point is the mean of three observations, vertical bars represent SE.

percentage basis, in the second experiment than in the first experiment, but grasshoppers had no effect on percentage loss of N (Table 1).

Experiment and grasshoppers had significant effects on the nitrogen harvest index (Table 1). Averaged over

Fig. 4. Regression of below-ground dry matter (A, at anthesis, and B, at maturity), difference in below-ground dry matter between anthesis and maturity as a percentage of dry matter present at anthesis (C), and root surface area at maturity (D) on numbers of grasshoppers per pot. Each point is the mean of three observations, vertical bars represent SE.

all grasshopper levels, N harvest index was 0.58 and 0.76 for exp. 1 and 2, respectively. Nitrogen harvest index declined with increasing grasshopper densities, although, as with dry matter harvest index, the effect was not pronounced. When corrected for effect of experiment, N harvest index declined by only 0.010 per grasshopper.

DISCUSSION

Grasshoppers may damage barley (or other small grains) by removal of photosynthetic tissue or, later in the season, by head clipping (Pickford and Mukerji 1974; Wright 1986; Begna and Fielding 2005). In this study of gradual, season-long defoliation, leaves, and later in the season, awns and glumes, were the most damaged parts of the plant. Yield loss was proportionally less than the reduction in leaf area due to grasshoppers; at the highest levels of grasshopper feeding, leaf area was reduced by 42 to 50% in the two experiments, compared with controls, whereas grain yield was reduced by 28 to 43%. This is not unexpected because most above-ground tissues of barley plants, not just the leaves, are photosynthetically active. Also, partial defoliation may allow more light to penetrate to the lower leaves, which could compensate for the loss of leaf area (Higley 1992). In soybeans, defoliation up to 33% has been shown to be tolerated with little impact on yield (Higley 1992; Haile et al. 1998).

The results of this experiment, conducted in controlled environment chambers, compare favorably with results from field experiments (Begna and Fielding 2005). Grain yields in the absence of grasshoppers in the present study were equivalent to about 310 g m⁻². In the field, yields without grasshoppers averaged 352 g m⁻² in 2002, a year with good growing conditions. In 2003, in which plants experienced early-season drought, yields averaged only 157 g m⁻². Yield losses in the present study were also similar to results from the field studies: slopes of the regression of yield on grasshopper numbers were 1.1 and 1.6 in the indoor exps. 1 and 2, respectively; and, in the field experiments, slopes were 1.9 and 1.4, in 2002 and 2003, respectively (Begna and Fielding 2005).

Although there were differences in plant growth parameters between the two experiments, they did not appear to be related to any differences in grasshopper feeding. Overall, the size of the plants in exp. 2 was generally smaller. Nevertheless, the smaller plants in the second experiment were able to produce similar grain crops as in the first experiment, perhaps by proportionally greater translocation of carbohydrates and protein to the developing grain. Above-ground plant biomass (excluding grain) and nitrogen declined from shortly after anthesis to physiological maturity to a greater degree in the second experiment than in the first experiment. Some of that loss was probably due to respiration, grasshopper consumption and dropped leaves, but much of the difference would be accounted

for translocation to the developing grain (Gallagher et al. 1976).

Pickford and Mukerji (1974) reported greater yield losses in wheat with earlier introduction of grasshoppers, but only at the highest densities (equivalent to more than 100 grasshoppers m⁻²). Other studies have examined the effect of timing of defoliation on yield of barley or wheat, but most of these have been one-time, drastic defoliation events rather than gradual defoliation similar to insect feeding. Jenkyn and Anilkumar (1990) found that grain yield of barley plants was most sensitive to severe defoliation at early tillering stages and later after the flag leaf began to emerge. Mukerji et al. (1976) and Olfert and Mukerji (1983), studying the effect of severe, short-term defoliation of wheat by grasshoppers, determined that, in general, earlier defoliation had a greater effect than later defoliation events. In light of our study, it appears that timing of initiation of defoliation is not as important when defoliation is gradual, except at very early stages when the above-ground plant tissues may be completely consumed by large numbers of young grasshoppers (Begna and Fielding 2003). In the current study, the grasshoppers were small (3rd instars) when introduced. Feeding by grasshoppers increases proportionally with size (Parker 1930) and so loss of plant tissue remains relatively light until the grasshoppers reach 5th instar or adults.

The indirect effects of grasshoppers on below-ground plant growth were revealed in the reduced dry weight of roots shortly after anthesis in both experiments and at maturity in the second experiment. Estimates of root surface area did not reflect the reduction in below-ground dry matter, at least at anthesis, suggesting that the lower root mass associated with grasshopper feeding may have been a result of reduced storage of photosynthates. Crops with a well-established root system may be able to utilize localized supplies of available soil water and nutrients and successfully compensate for plant tissue losses and also compete more successfully with weeds.

Grasshopper feeding reduced the overall growth and yield of the plants, but did not appear to greatly alter the relationships between leaves, stems, roots, and grain. The barley plants were able to maintain relatively constant proportions of grain, leaves and stems, and roots over all levels of grasshopper damage. Although feeding was confined to above-ground parts and roots were only indirectly damaged, grasshopper feeding did not have a significant effect on the root:shoot ratio. Apparently root growth slowed enough and relatively more assimilates were allocated to above-ground growth to maintain a constant ratio of above- to below-ground dry matter. A general response to defoliation by insects and/or vertebrates is to allocate more resource to shoot than roots (Ryle and Powell 1975; Meyer 1998; Guitian and Bardgett 2000). In addition, grasshopper feeding did not affect the harvest index based on dry matter, but the nitrogen harvest index was affected by grasshopper

feeding, with a slightly higher harvest index with increasing grasshoppers.

Bidinger et al. (1977) and Austin et al. (1980) found that barley plants stressed by drought post-anthesis relied on pre-anthesis assimilation to maintain grain yields to a greater degree than non-stressed plants. In contrast, season-long grasshopper feeding would tend to reduce assimilation of C equally before and after anthesis, and thus the relative amounts of pre- and post-anthesis assimilates would be unaffected by grasshopper feeding. In addition, grasshoppers apparently did not influence the proportions of C or N translocated or lost after anthesis. Assuming that post-anthesis consumption of plant tissue by grasshoppers was not negligible, we expected that there would be relatively less non-grain dry matter remaining at maturity (higher harvest index) because of grasshopper consumption and perhaps greater translocation of dry matter to the developing grain, but this was not the case. Apparently, adjustments were made by the plant to maintain constant proportions despite post-anthesis consumption of plant tissue by the insects.

The reduction in grain yield due to grasshoppers was a combination of a shortage of assimilates reaching the sink (grain), resulting in lower grain weights, and fewer kernels. Other studies of defoliation in small-grains have shown that yield reduction is primarily due to smaller grains, rather than fewer grains (Ryle and Powell 1975; Olfert and Mukerji 1983; Aggarwal et al. 1990). In the present study, pre-anthesis feeding by grasshoppers may have reduced the number of fertile spikelets, thus reducing grain number. Nitrogen (therefore protein content) per kernel remained more or less constant with increasing grasshopper damage. Each embryo probably requires some minimum amount of protein to be viable, thus plants allocated a fairly constant amount of protein to each seed.

Barley plants are robust and capable of compensating for loss of leaf tissue and less than ideal growing conditions. In the second experiment, grain yield was apparently supported to a greater degree by translocation of assimilates. The percentage loss of above-ground and below-ground dry matter from anthesis to maturity was greater in the second experiment than in the first, and harvest indices were greater in the second experiment. Also, only in the second experiment did grasshoppers have an effect on loss of dry matter from anthesis to maturity. In summary, grasshopper feeding reduced leaf area and above-ground dry weight directly by destruction of plant tissues and indirectly by reducing growth rate of the plant. Reduction of below-ground biomass was likely due to reduced growth and decreased allocation of assimilates to the roots. These results provide greater understanding of plant responses to insect feeding damage and will lead to more accurate estimates of economic injury levels. Close agreement with field results (Begna and Fielding 2005) lends

support to estimates of yield loss to grasshopper damage.

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